MORPHOLOGICAL VARIATION IN PARDOSA PRATIVAGA L. KOCH, 1870, P. PRATIVAGA VAR. FULVIPES COLLETT, 1875 AND P. PULLATA CLERCK, 1757 (ARANEAE, LYCOSIDAE)

by

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Abstract

Specimens of *Pardosa prativaga* (L. Koch, 1870), *Pardosa prativaga* var. *fulvipes* (Collett, 1875), and *Pardosa pullata* (Clerck, 1757) were sampled from several populations in the Netherlands. Measurements were carried out relating to the cephalothorax, the epigyne and the first and fourth legs. The results are discussed in the context of character displacement and hybridisation.

Introduction

In the genus *Pardosa* four groups of species are usually distinguished: the *amentata* group, the *monticola* group, the *paludicola* group and the *pullata* group (Locket & Millidge, 1951; Wiebes, 1959). This division is based exclusively on external morphological characters, especially the shape of the external genitalia and the design and colour of the cephalothorax. The group of *P. pullata* contains the species *P. prativaga* (L. Koch, 1870), including *P. prativaga* var. *fulvipes* Collett, 1875, and *P. pullata* (Clerck, 1757) (Locket & Millidge, 1951; Wiebes, 1959). According to these authors the species can be differentiated by the annulation and spinosity of the legs and the shape of the external genitalia.

It is worth noticing that several other species names have been proposed for specimens closely resembling *P. prativaga: P. femoralis* Simon, 1876, *Lycosa montivaga* Kulczynski, 1898, *P. kervillei* Simon, 1932 and *Lycosa riparia* C. L. Koch, 1833 (Tongiorgi, 1966). The fact that these names have been applied to what is probably one species may be due to the highly variable morphology of *P. prativaga.*

The shape of the external genitalia of females, the epigyne, of some species of the *P. pullata* group was studied by Petrusewicz (1935). He investigated *Lycosa riparia* C. L. Koch, 1833, *Lycosa riparia* var. *sphagnicola* Dahl, 1908, and *Lycosa montivaga* Kulczynski, 1898. Although Petrusewicz gave no quantitative data, he was able to show that variation in the shape of the epigyne was such that no discontinuities between the species studied exist. He concluded that *L. montivaga* is only a subspecies of *L. riparia* and that this species is identical with *L. riparia* var. *sphagnicola* (= *Lycosa prativaga* var. *fulvipes* Collett).

The aim of the present study is to investigate and describe the variability of several morphological characters of the *P. pullata* group both at the species and population level,

within a limited area (the Netherlands). In this country *P. pullata* is most widespread; it occurs in all provinces. The same is true for *P. prativaga* although this species is mainly found in the southwestern part of the Netherlands. *P. prativaga* var. *fulvipes* has not been found before in our country (Wiebes, 1959) but now we have found this species in all provinces along the frontier of the Netherlands and Germany.

On the basis of this detailed study the problems in the classification of the species of this group are illustrated and, to some extent, evaluated.

Materials and Methods

Specimens of the *P. pullata* group were sampled from several populations in the Netherlands (Table 1). They were identified by the colour of the cephalothorax and the abdomen. The following key was used (Wiebes, 1959; Tongiorgi, 1966; Locket and Millidge, 1951):

Females reddish, males dark *(P. pullata),*
Females greyish, males greyish brown *(P. prativaga),*
Females and males reddish, lighter than *P. pullata* females *(P. prativaga* var. *fulvipes).*

locality	pullata ♀	pullata ♂	prativaga ♀	prativaga ♂	fulvipes ♀	fulvipes ♂
Lange pad, Oostvoorne mowed field, wet	-		A 36		-	
Groene strand, Oostvoorne higher grass, moist	+		B 22		-	
Bosweitje, Rockanje mowed grass, wet	K 90	35	C 58	20	-	
A'veense poel, Bovenkerk marshy grassland	L 21		D 40	20	-	
de Eese, Steenwijk peat-moor swamp	+		-		E 51	30
Hollandse Rading, Hilversum, moorland, grown with moss	F 51		-		-	
Arnica weitje, Schiermonnikoog, marshy grassland	G 40	20	-		-	
Bergvennen, Denekamp peat-moor swamp	H 68		-		+	
Total number per subgroup	270	55	156	40	51	30

Table 1. Classification of the populations of the *P. pullata* group with the number of specimens collected. A-L: sample code; — specimens of this subgroup are not present in this population; + some specimens of this subgroup are present in this population

The populations of the *P. pullata* group were classified into three subgroups with the help of these specific criteria: the *pullata, prativaga* and *fulvipes* subgroup. Both the subgroup *pullata* and the subgroup *prativaga* occurred in pure as well as in mixed populations (Table 1).

The determination based on the colour of both the cephalothorax and the abdomen, was checked by recording the following characters.

(a.) The number of retrolateral spines on the tibia and metatarsus of the first leg. Wiebes (1959) used this character to separate *P. pullata* from *P. prativaga*. For *P. prativaga* he mentions the presence of two retrolateral spines on the tibia and one on the metatarsus of the first leg. *P. pullata* would not have any spines there.

(b.) The presence of dark rings on the tibia and metatarsus of the first leg. This annulation is typical for *P. prativaga* (Wiebes, 1959).

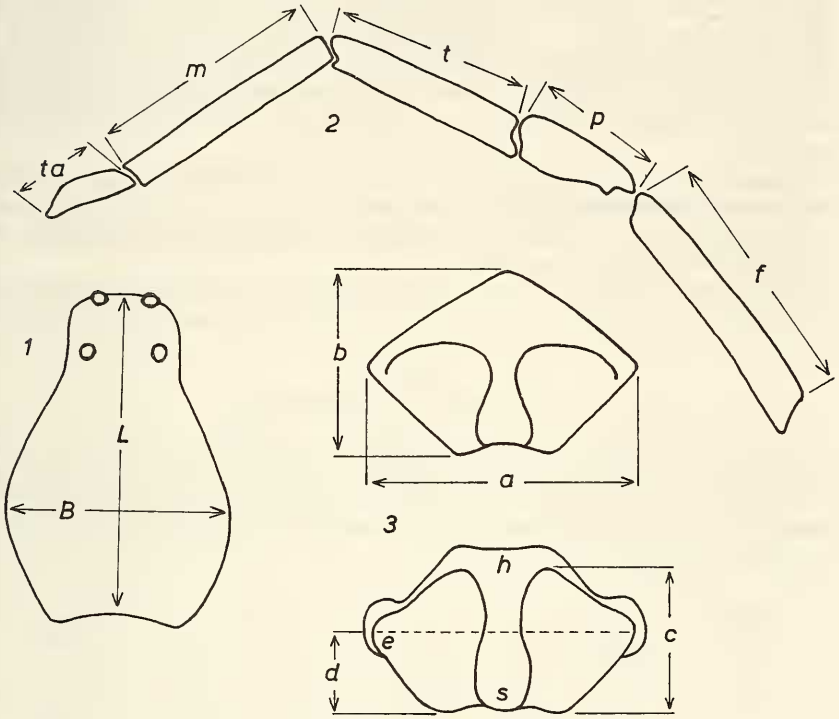

Fig. 1. The measured characters of the specimens of the *P. pullata* group. 1, the cephalothorax length (L) and width (B); 2, the leg, the femur (f), patella (p), tibia (t), metatarsus (m) and tarsus (ta); 3, the epigyne, the width (a) and height (b), the length of the septum (c) and the length of the part of the septum below the imaginary line through the lateral pockets (d). h: hat, s: septum, e: lateral pocket ("ear")

On the basis of this classification the following characters, generally used in the description of lycosid spiders, were measured (Fig. 1).

Cephalothorax: length and width.

Leg: the length of femur, patella, tibia, metatarsus and tarsus of the first and fourth legs. The method of Cooke (1965) was used so that the total length of the leg is the sum of the lengths of the parts.

Epigyne: width and height, the length of the septum and the length of the part of the septum below the imaginary line through the lateral pockets. The last mentioned measure in relation to the total length of the septum, was used as a measure for the

shape of the anterior margin of the epigyne. The shape of this margin was used to separate *P. prativaga* from *P. pullata* by Dahl (1908) and Palmgren (1939). According to these authors the anterior margin of the epigyne of *P. pullata* runs backward to the outside, that of *P. prativaga* straight and that of *P. prativaga* var. *fulvipes* forward to the outside.

Measurements, given in micrometer units (MU), were performed with a Reichert stereomicroscope at a magnification of 6.3 × 4 for the measures of the cephalothorax and the legs (accuracy 2.3%) and at magnification of 6.3 × 10 for the measures of the epigyne (accuracy 5.0%). At a magnification of 6.3 × 4 one μ is 0.042 mm, at 6.3 × 10 one μ is 0.017 mm. All measurements were made in the plane of focus: e.g. with measurements on the length of the cephalothorax both the anterior margin of the eyes and the posterior lobes of the cephalothorax were in the plane of focus at the same time.

Duncan's new multiple range test with Kramer's modification for inequal sample size was used for statistical analysis (Weber, 1967).

Microphotographs were made of the epigynes of some females of every sample with a Zeiss photomicroscope at magnification of 40 ×.

As yet it was impossible to measure the palpal organs of the males. These organs are very complex and the structure of the palps of the species studied seems to be very similar.

RESULTS

The spination and annulation

The distribution of retrolateral spines on the first leg is given in Table 2. This table shows that in the subgroup *prativaga* two retrolateral spines occur on the tibia and one on the metatarsus. In females of this subgroup specimens occur which show only one retrolateral spine on the tibia. In males, however, sometimes two retrolateral spines on the metatarsus are found.

number of spines	subgroup:	prativaga				pullata					fulvipes
t - mt	sample:	A	B	C	D	F	G	H	K	L	E
0 - 0		.	.	.(.)	.(.)	19	10(18)	20	16(35)	9	1(.)
0 - 1		.	.	.(.)	.(.)	1	.(2)	.	2(.)	.	1(.)
1 - 0		.	.	.(.)	.(.)	.	.(.)	.	1(.)	1	.(.)
1 - 1		2	2	.(.)	3(.)	.	.(.)	.	1(.)	.	6(2)
2 - 1		8	8	18(11)	7(12)	.	.(.)	.	.(.)	.	12(22)
2 - 2		.	.	1(9)	.(7)	.	.(.)	.	.(.)	.	.(5)
2 - 0		.	.	1(.)	.(1)	.	.(.)	.	.(.)	.	.(1)
number:		10	10	20(20)	10(20)	20	10(20)	20	20(35)	10	20(30)

Table 2. The distribution of retrolateral spines on the tibia (t) and metatarsus (mt) of the first leg in the *P. pullata* group (males in parenthesis)

In the subgroup *pullata* retrolateral spines on the tibia and the metatarsus are nearly always absent. Especially in females of this subgroup (sample K, mixed population), specimens are found with one retrolateral spine on the tibia and the metatarsus.

The spination of the first leg in the subgroup *fulvipes* is comparable to that in the

subgroup *prativaga*. However, especially in females, more specimens occur with less than two (sometimes even none) retrolateral spines on the tibia and no retrolateral spine at all on the metatarsus.

The presence of annulation on the tibia and metatarsus of the first leg was also recorded in the specimens used for the study of the above features. All the females and all the males except one (sample D, mixed population) of the *prativaga* subgroup show this annulation which is absent in all the specimens of the subgroups *pullata* and *fulvipes*. Only two females (sample K, mixed population) in the subgroup *pullata* showed more or less clear dark rings on the tibia and the metatarsus.

So the spination, the annulation of the legs, and the colour of cephalothorax and abdomen — when used as taxonomic features — yield a similar division of the *P. pullata* group into three subgroups.

The cephalothorax

Frequency distributions for the measures of the cephalothorax of both males and females are given in Fig. 2. Table 3 presents the means and standard deviations of these measures. The results of Duncan's test are given in Fig. 4A.

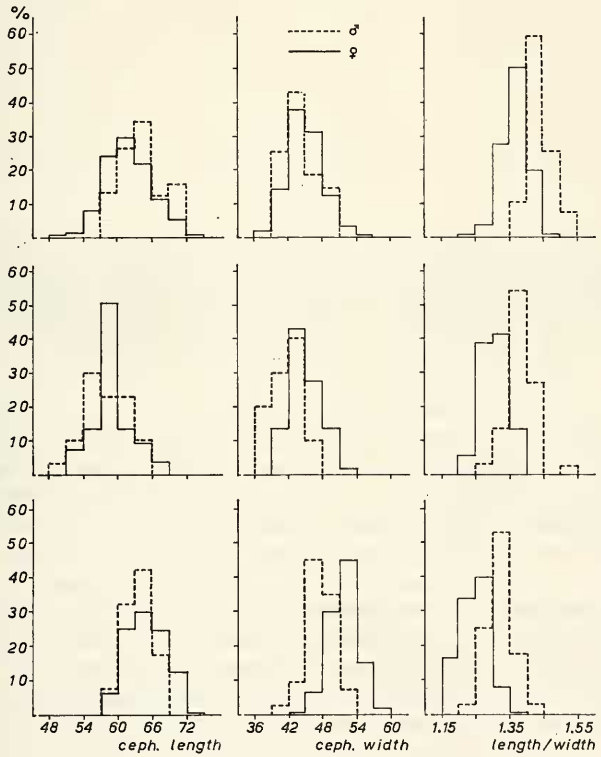

Fig. 2. Frequency distributions of the cephalothorax length, the cephalothorax width and the ratio of these lengths. The figures are given in micrometer units. Below: subgroup *prativaga;* in the middle: subgroup *fulvipes;* at the top: subgroup *pullata*

Comparison of the subgroups gives the following result. The subgroup *prativaga* shows higher mean values for the length and width of the cephalothorax than the subgroups *fulvipes* and *pullata*. The latter subgroups do not differ much with respect to these measures (Table 3). Considerable overlaps between the subgroups do occur (Fig. 2). The values for the ratio of the length and the width of the cephalothorax are highest in the subgroup *pullata*, lowest in the subgroup *prativaga* and intermediate in the subgroup *fulvipes* (Table 3).

	L ♀		♂		B ♀		♂		L/B ♀		♂	
	M	s.d	M	s.d	M	s.d	M	s.d	M	s.d	M	s.d
prat.	65.5	2.7	63.9	2.2	52.3	2.4	48.3	1.8	1.25	0.04	1.32	0.03
fulv.	59.6	3.4	58.6	3.7	45.4	2.7	42.3	2.7	1.31	0.04	1.39	0.04
pull.	62.3	3.6	64.9	3.4	45.5	2.8	45.0	2.5	1.37	0.04	1.44	0.03
A	64.4	3.1			52.2	2.9			1.23	0.04		
B	63.8	2.6			51.1	2.5			1.25	0.04		
C	64.9	3.0	62.7	2.5	52.2	2.5	47.0	1.9	1.25	0.05	1.33	0.04
D	68.4	2.1	65.1	1.7	53.3	1.9	49.6	1.7	1.28	0.04	1.31	0.03
E	59.6	3.4	58.6	3.7	45.4	2.7	42.3	2.7	1.31	0.04	1.39	0.04
F	61.2	4.3			44.5	3.4			1.37	0.04		
G	61.2	3.5	63.2	3.1	44.4	2.7	43.4	2.7	1.37	0.03	1.46	0.04
H	60.8	2.8			44.3	2.3			1.38	0.04		
K	63.8	4.0	65.9	3.5	47.0	3.0	45.9	2.7	1.36	0.04	1.44	0.03
L	65.1	3.2			47.1	2.4			1.39	0.03		

Table 3. Measures of the cephalothorax in the *P. pullata* group. Mean values (M) and standard deviation (s.d.) for the length (L), width (B) and ratio of length and width (L/B) for the males and the females of the respective subgroups and the individual samples. *prat.:* subgroup *prativaga* containing the samples A, B, C and D; *fulv.:* subgroup *fulvipes* containing sample E; *pull.:* subgroup *pullata* containing the samples F, G, H, K and L

A comparison of males and females (Table 3) shows that, in the *P. pullata* group, males are more slender than females. In the subgroup *pullata* this is caused by the higher value for the length of the cephalothorax in males than in females. In the subgroups *prativaga* and *fulvipes* the width of the cephalothorax is smaller in males than in females.

The results of the statistical analysis of the above differences are as follows (Fig. 4). Samples of *prativaga* from pure populations (samples A and B) differ significantly from *pullata* samples from pure populations (samples F, G and H). The values for the width and length of the cephalothorax are significantly higher in samples from mixed populations than in samples from pure populations (subgroups *prativaga* and *pullata*, males and females). The samples of the respective subgroups differ significantly, with regard to the ratio of the length and the width of the cephalothorax. Again, in females, the values for samples from mixed populations deviate from those of samples from pure populations (subgroup *pullata:* sample K — samples G, H and L; subgroup *prativaga:* sample D — samples A and B).

The first and fourth legs

The femur, patella, tibia, metatarsus and tarsus of the first and fourth left legs were measured for all males and for ten females taken at random from every sample. The sum of these lengths was taken as the total length of the leg. The ratio of the length of the fourth and that of the first leg was calculated. The data are given in Table 4 and Table 5. Fig. 4 B presents the results of Duncan's test.

	leg I				leg IV				leg IV/ leg I			
	♀		♂		♀		♂		♀		♂	
	M	s.d	M	s.d	M	s.d	M	s.d	M	s.d	M	s.d
prat.	174	9.5	168	7.2	249	13.9	227	9.6	1.42	0.04	1.35	0.07
fulv.	152	9.2	148	11.0	220	14.2	201	13.5	1.43	0.01	1.36	0.03
pull.	143	8.2	136	7.1	213	11.7	208	11.2	1.49	0.03	1.53	0.05
A	172				233				1.35			
B	167				240				1.43			
C	177		166		253		223		1.43		1.34	
D	181		171		261		232		1.44		1.36	
E	152		148		220		201		1.43		1.36	
F	139				207				1.48			
G	138		132		201		200		1.45		1.53	
H	142				218				1.50			
K	143		138		214		212		1.49		1.54	
L	151				227				1.50			

Table 4. Measures of the legs in the *P. pullata* group. The length of the first (leg I) and the fourth leg (leg IV) and the ratio of these lengths. Mean (M) and standard deviation (s.d.) are given for the respective subgroups; for the individual samples only means are given. *prat.:* subgroup *prativaga* containing the samples A, B, C and D; *fulv.:* subgroup *fulvipes* containing sample E; *pull.:* subgroup *pullata* containing the samples F, G, H, K and L

The results with respect to the distinct subgroups are as follows. The subgroup *prativaga* shows longer first and fourth legs than the subgroups *fulvipes* and *pullata,* in males as well as in females. Moreover, the first leg is longer in the *fulvipes* subgroup than in the *pullata* subgroup (Table 4). These differences in leg lengths reflect differences in the lengths of the tibia and the metatarsus mainly, although all parts of the legs are, to some extent, involved (Table 5). The specimens of the *pullata* subgroup show relatively short first legs, i.e., the ratio of the length of the fourth and that of the first leg is high in this subgroup (Table 4).

A comparison of males and females shows that, in each subgroup, males have shorter legs than females (Table 4). With respect to the first leg these differences are due to differences in the lengths of all parts of the leg, except in the subgroup *prativaga.* In this subgroup the differences are mainly due to the length of the femur. As regards the fourth leg, males and females differ with respect to the lengths of the femur, tibia and metatarsus, except in the subgroup *pullata,* in which all parts of the leg are concerned.

The differences in leg length between males and females are most conspicuous for the length of the fourth leg in the subgroups *prativaga* and *fulvipes.* In these subgroups,

sample	f-1	p-1	t-1	m-1	ta-1	f-4	p-4	t-4	m-4	ta-4
A ♀	47.4	22.5	39.0	38.5	24.6	60.8	23.1	51.1	67.8	29.7
B ♀	46.7	21.5	37.5	37.0	24.2	60.6	22.8	51.8	72.0	32.5
C ♀	48.6	23.6	39.7	39.4	25.4	63.3	24.2	55.0	76.5	33.8
♂	43.6	20.2	38.2	40.4	24.1	56.5	21.7	47.5	67.0	30.0
D ♀	49.5	22.6	41.6	41.6	26.1	65.4	24.5	56.5	78.7	35.7
♂	44.1	21.1	39.1	41.1	25.6	55.9	22.8	48.8	69.3	32.3
E ♀	41.9	20.0	34.2	32.8	22.1	56.2	21.1	47.2	64.1	29.5
♂	40.5	18.4	33.8	34.2	21.6	51.7	19.4	43.4	59.6	27.3
F ♀	37.8	20.0	30.0	30.0	21.4	50.2	20.2	44.0	62.5	30.2
G ♀	38.4	19.8	29.9	28.9	20.6	50.6	19.9	42.1	59.5	28.7
♂	37.2	19.1	27.6	28.2	20.0	50.1	19.9	41.3	60.1	28.9
H ♀	39.6	19.8	30.6	30.0	21 6	55.4	21.6	44.9	63.1	29.3
K ♀	40.2	20.5	31.2	30.1	21.3	52.6	21.2	45.7	64.5	30.4
♂	39.1	20.1	29.1	29.2	20.5	52.9	21.0	43.9	63.9	29.8
L ♀	41.6	21.2	33.0	33.0	22.5	57.5	22.6	47.8	66.9	32.0

Table 5. Measures of the legs in the *P. pullata* group. Means are given per sample of the femur (f), patella (p), tibia (t), metatarsus (m) and tarsus (ta) of the first (1) and fourth (4) leg

the ratio of the length of the fourth and that of the first leg is lower in males than in females (Table 4).

The results of the statistical analysis of the differences in leg length are as follows (Fig. 4 B). Samples of *prativaga* generally differ from *pullata* samples with respect to all the measures. Besides, the subgroup *pullata* differs clearly from the subgroups *prativaga* and *fulvipes* with respect to the ratio of the length of the fourth and that of the first leg. Several samples, both within the subgroup *prativaga* and the subgroup *pullata,* differ significantly with regard to the lengths of the first and the fourth legs. These differences are due to the deviating values in the samples from the mixed populations (in females: samples D and L; in males: sample K; see Table 1). The values for the sample of the *fulvipes* subgroup correspond to those of the *pullata* samples from mixed populations.

The epigyne

Frequency distributions for the measures of the epigyne of females of the *P. pullata* group are given in Fig. 3. Table 6 presents the means and standard deviations of these measures. The results of Duncan's test are given in Fig. 4 C.

The results are as follows with respect to the distinct subgroups. In general, the values of the measures in the subgroup *pullata* are significantly higher than those in the subgroups *prativaga* and *fulvipes* (Table 6). Especially with respect to the values of the width of the epigyne and the length of the septum, the overlap between these subgroups is small (Fig. 3). Although the values in the subgroup *fulvipes* are, generally,

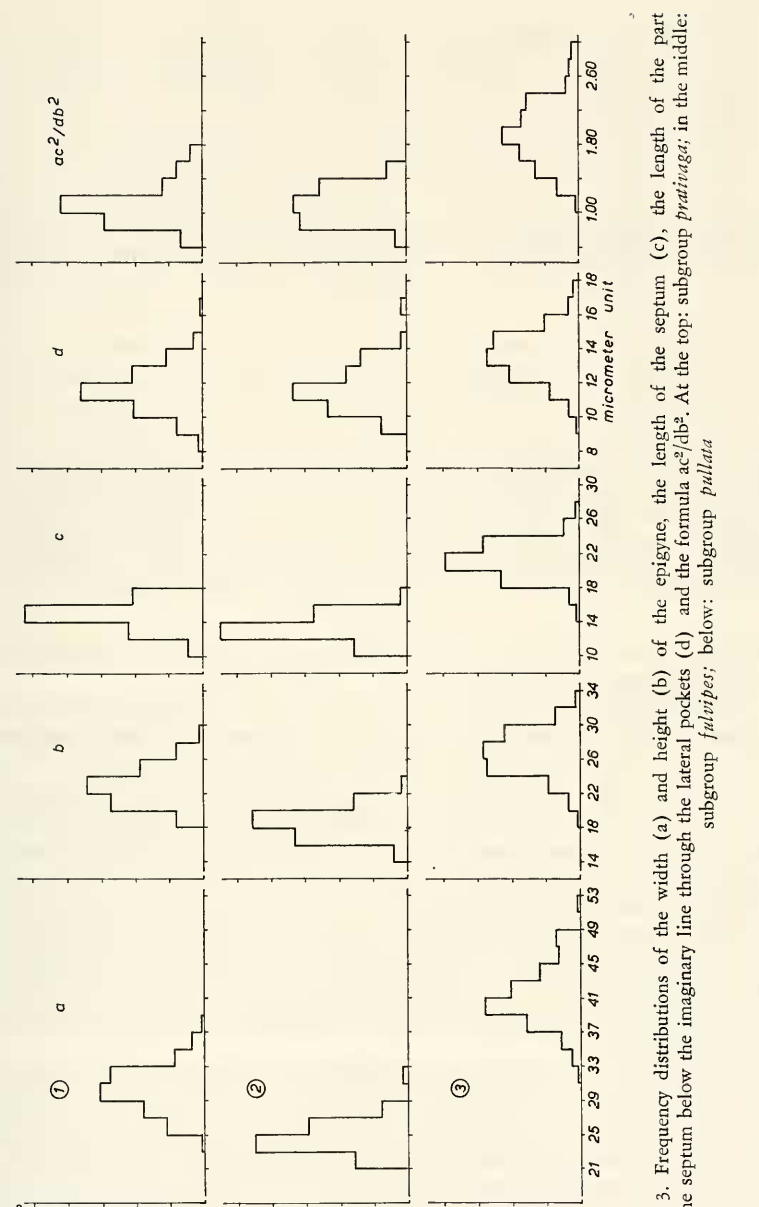

Fig. 3. Frequency distributions of the width (a) and height (b) of the epigyne, the length of the septum (c), the length of the part of the septum below the imaginary line through the lateral pockets (d) and the formula ac^2/db^2. At the top: subgroup *prativaga*; in the middle: subgroup *fulvipes*; below: subgroup *pullata*

code:	a		b		c		d		ac^2/db^2		d/c
	M	s.d	M	s.d	M	s.d	M	s.d	M	s.d	M
prat.	31.0	2.3	23.3	2.2	15.3	1.4	12.3	1.2	1.09	0.20	0.81
fulv.	25.1	2.0	19.1	1.3	13.8	1.3	12.2	1.4	1.10	0.18	0.92
pull.	41.2	2.7	26.9	2.2	21.6	1.7	14.0	1.4	1.92	0.35	0.64
A	31.3	2.4	23.0	2.2	15.1	1.4	11.9	1.1	1.15	0.23	0.79
B	29.1	2.4	22.2	1.7	14.6	1.6	11.4	1.0	1.13	0.29	0.80
C	30.6	2.3	23.3	2.2	15.3	1.4	12.6	1.3	1.05	0.19	0.84
D	32.2	1.9	24.8	1.3	15.9	1.1	12.6	1.3	1.06	0.13	0.79
E	25.1	2.0	19.1	1.3	13.8	1.3	12.2	1.4	1.10	0.18	0.92
F	38.9	2.7	25.3	3.0	20.6	2.0	12.9	1.4	1.97	0.41	0.64
G	41.1	2.3	26.6	2.2	22.0	1.4	14.2	1.1	2.00	0.30	0.64
H	41.4	2.3	27.6	2.0	21.4	1.4	14.0	1.1	1.83	0.31	0.64
K	41.4	3.0	26.7	2.0	21.8	2.0	14.2	1.3	1.98	0.40	0.66
L	45.7	3.2	29.0	2.0	22.8	1.9	15.3	1.3	1.88	0.42	0.64

Table 6. Measures of the epigyne in the *P. pullata* group. Mean value (M) and standard deviation (s.d.) for the width (a) and height (b) of the epigyne, the length of the septum (c) and the length of the part of the septum below the imaginary line through the lateral pockets (d), the ratio ac^2/db^2 and the ratio d/c. The figures are given for the respective subgroups and for the individual samples. *prat.:* subgroup *prativaga* containing the samples A, B, C and D; *fulv.:* subgroup *fulvipes* containing the sample E; *pull.:* subgroup *pullata* containing the samples F, G, H, K and L

significantly lower than those in the subgroup *prativaga,* these subgroups show a considerable overlap (Table 6).

Significant differences exist between samples within the subgroups (Fig. 4 C). These differences are due to deviating values for the samples D, L (mixed populations of *prativaga* and *pullata,* respectively) and F (pure population of *pullata).*

The shape of the anterior margin of the epigyne is reflected by the ratio of the length of the part of the septum below an imaginary line through the lateral pockets (Table 6, d) and the length of the septum (Table 6, c; d/c). This ratio was calculated for ten females taken at random from every sample. The lowest values occur in the subgroup *pullata,* the highest in the subgroup *fulvipes.* Some overlaps in the ranges of this measure exist between the subgroup *prativaga* on the one hand and the subgroups *pullata* and *fulvipes* on the other hand. The latter subgroups show no overlap. Thus, the anterior margin of the epigyne in the subgroup *pullata* runs clearly backward to the outside. That in the subgroup *prativaga* and *fulvipes* runs less backward or even forward to the outside, respectively.

The overall shape of the epigyne is expressed in the formula ac^2/db^2. This formula contains the measures *a* (the width of the epigyne), *b* (the height of the epigyne), *c* (the length of the septum) and *d* (the length of the part of the septum below the imaginary line through the lateral pockets). In composing this formula, these measures are used in the following way: a/b expressing the form of the epigyne (circular or oblong), c/b expressing the relative length of the septum (this measure reflects the development of the hat of the epigyne), d/c expressing the shape of the anterior margin of the epigyne ($a/b \times c/b : d/c = ac^2/db^2$).

The value of this measure in the subgroup *pullata* is twice as large as that in the subgroups *prativaga* and *fulvipes* (Table 6). It is striking that the samples of the subgroup

sample:	subgroup:	a	b	c	d	ac^2/db^2
D and F	prativaga-pullata	6.7	0.9	4.7	0.3	0.91
F and L	pullata -pullata	6.6	3.5	2.3	2.6	0.09
D and B	prativaga-prativaga	2.2	0.3	0.7	1.0	0.07
B and E	prativaga-fulvipes	3.8	2.9	0.8	0.7	0.03
D and E	prativaga-fulvipes	6.0	5.2	1.5	0.3	0.04

Table 7. Differences in mean value of the measurements of the epigyne between the samples B, D (subgroup *prativaga*), E (subgroup *fulvipes*), F and L (subgroup *pullata*). a, b, c and d: see table 6

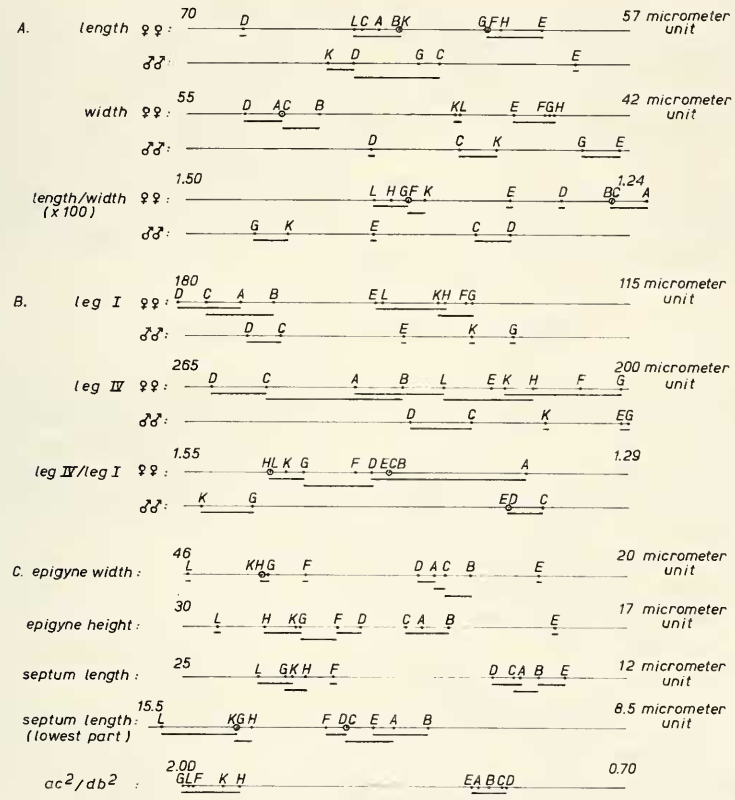

Figure 4. The results of Duncan's test applied to the measures of the cephalothorax (A), the length of the first and fourth leg (B) and the epigyne (C). The samples are arranged from the left to the right according to decreasing mean value. The distance between the samples corresponds to the difference in mean value. The samples which are not underlined together, differ significantly ($\alpha = 0.01$). The samples A, B, C and D belong to the subgroup *prativaga* (C and D from mixed populations), sample E belongs to the subgroup *fulvipes* and the samples F, G, H, K and L belong to the subgroup *pullata* (K and L from mixed populations)

pullata are clearly separated from those of the subgroups *prativaga* and *fulvipes* with regard to this measure. Moreover, the differences between samples within any of the subgroups are small and not significant (Fig. 4). So, interpopulation variation is small. On the other hand interpopulation variation is large for the more specific features of the epigyne (see above and Table 7). On the contrary, intrapopulation variation is larger for the formula ac^2/db^2 than for the special features which compose this formula (Table 6).

To illustrate the above points, microphotographs were made of the epigynes of three females of every sample (Plates 1, 2). The size of the epigyne, the size and shape of hat and septum and the shape of the anterior margin of the epigyne show continuous variation in the *P. pullata* group (Photographs L-1, F-1, F-3, G-1, B-2, A-3, C-3, K-1, D-3, E-3).

Female K-1 (*pullata,* mixed population) takes a peculiar place in this series. This female was identified as *pullata* specimen by the reddish body colour, but the epigyne cannot be classed either in the *pullata* or in the *prativaga* subgroup. Moreover, this female showed *prativaga* features (annulated legs), *pullata* features (one retrolateral spine on the tibia, no retrolateral spines on the metatarsus) and intermediate features (cephalothorax length/width = 1.30, $ac^2/db^2 = 1.41$, length leg IV/leg I = 1.46). According to Locket & Millidge (1951), the occurrence of specimens intermediate between *pullata* and *prativaga* reflects interbreeding in the field. Moreover, matings of specimens of respective species have been observed, despite the apparent specific courtship behaviour in the genus *Pardosa* (Vlijm & Dijkstra, 1966).

General conclusions and discussion

Specimens of the *P. pullata* group, sampled from several populations in the Netherlands, were grouped into three subgroups: the *pullata,* the *prativaga* and the *fulvipes* subgroup. This was done on the basis of the colour of the cephalothorax and the abdomen. This rather subjective method was tested by recording the spinosity and annulation of the tibia and the metatarsus of the first left leg. The combination of these data results in the following scheme:

1. *pullata* subgroup, corresponding to *P. pullata* (Clerck):
   colour: females reddish, males dark
   spination: retrolateral spines absent
   annulation: absent
2. *prativaga* subgroup, corresponding to *P. prativaga* (L. Koch):
   colour: females greyish, males greyish brown
   spination: mostly two retrolateral spines on the tibia and one on the metatarsus
   annulation: present
3. *fulvipes* subgroup, corresponding to *P. prativaga* var. *fulvipes* (Collett):
   colour: females and males reddish, more light than *pullata* females
   spination: one or two retrolateral spines on the tibia and one on the metatarsus
   annulation: absent

In the animals thus classified, measurements were carried out relating to the cephalothorax, the epigyne and the first and fourth legs. Frequency distributions of the measures of the cephalothorax and the epigyne were established for each subgroup. Differences between samples with respect to these measures were tested with

Duncan's new multiple range test. The results were used to evaluate the classification of the *P. pullata* group.

A considerable overlap exists between the respective subgroups with respect to the frequency distributions of the characters measured, in males as well as in females. The overlap is less conspicuous in the measures of the epigyne.

The results of Duncan's test show that several samples differ significantly regarding several measures. In some cases the differences between the samples within the subgroups are larger than those between the subgroups (epigyne). Especially samples from mixed populations (C, D: subgroup *prativaga;* K, L: subgroup *pullata*) differ from samples from pure populations of the same subgroup. Nonetheless, two groups of samples, corresponding to the *pullata* and the *prativaga* subgroups may be distinguished within the *P. pullata* group. The difference between these two groups is especially clear with respect to two measures: ac^2/db^2 (females: epigyne), and the ratio of the length of the fourth and that of the first leg. Differences between samples within subgroups do not occur with respect to these measures, whereas every sample of the *pullata* subgroup differs significantly from every sample of the subgroups *prativaga* (except in females, sample D) and *fulvipes.* The *fulvipes* sample does not differ significantly from the *prativaga* samples.

Grasshoff (1968) studied the variation in morphological characters in the *Araneus diadematus* group to show, ". . . wie man Arten anhand ausschliesslich morphologischer Kriterien biologisch sinnvoll abgrenzen kann . . ." According to him, the term morphospecies (Cain, 1954) must be used only when the variation of morphological characters is completely discontinuous. So only characters showing no overlap between species would be of systematic importance. The term morphospecies is used in contrast to the term biospecies, the latter referring to groups of individuals separated biologically rather than morphologically (Mayr, 1940). The present study shows that none of the measured characters is distributed discontinuously throughout the *P. pullata* group. The subgroups are no clear morphospecies.

Grasshoff states also that the genital morphological structures are species separating features with systematic priority. Thus he observed that intraspecific variation in the genital structures of the *Araneus diadematus* group is very small. In the *P. pullata* group only the formula ac^2/db^2 which is a measure of the overall shape of the epigyne shows a small interpopulation variation. However, the specific features combined in this formula show a large interpopulation variation. So it is improbable that the functional anatomy of the epigyne is involved in separating the species investigated. This is confirmed by the fact that males of the *prativaga* subgroup are able to copulate with females of the *pullata* subgroup. The resulting eggs are fertile (unpublished observations).

In this connection it seems to be very interesting that especially the samples from the mixed populations of the subgroups *prativaga* and *pullata* present difficulties to classification. This may be due to the occurrence of interbreeding in the field. Adaptations to a special type of habitat, however, could also account for this phenomenon because these mixed populations were found in specific habitats. Then these populations would consist of ecological races (genetically fixed differences) or ecophenotypes (differences not genetically fixed). Sample F is, probably, an example of adaptation to a specific habitat: the epigyne in this sample deviates considerably from that of other pure *pullata* populations.

According to Svärdson (1949) intraspecific variation will be small in closely related

species occurring in the same habitat. In this case the respective species will occupy different niches to escape interspecific competition. When only a single species occurs in a given habitat intraspecific variation will be large, because every part of the habitat will be used to escape intraspecific competition. The present study shows that variation in mixed populations is not clearly smaller than in pure populations. In addition, with respect to mean values, the differences are not larger between samples from sympatric populations than between those from allopatric populations as would be the case when character displacement is involved. So it is plausible that interbreeding is involved. Thus, the *P. pullata* group consists of two groups of populations which interbreed when they occur in the same habitat.

As to evolution in the *P. pullata* group, the habitat differences between the subgroups are important. Table 1 presents a rough description of the habitats of the populations studied. The table suggests that major habitat differences do not exist. According to Dahl (1908) *pullata* lives: "auf Humusreichen, mit kurzem Rasen bedeckten Boden", and *prativaga* "auf sumpfigen Wiesen". However, moist meadows are rich in humus. This agrees with the observation of Wiebes (1959) that *prativaga* occurs in fields and marshy soils and that *pullata* can be found in the same biotopes as *prativaga* but also in more dry places. At Vogelenzang, however, *prativaga* occurs in a very dry locality, grown with high, dense grass (Vlijm, Kessler, and Kessler-Geschiere, 1968). The habitat differences between populations of *prativaga* and *pullata* are obviously somewhat hazy. However, the subgroup *pullata* and the subgroup *prativaga* do clearly differ with regard to the ratio of the length of the fourth leg and that of the first leg. This ratio possibly depends on the habitat. This is especially plausible in the females carrying cocoons. This suggests that when the individuals of the two subgroups use similar habitats, they do this in a different way.

The position of the *fulvipes* subgroup in the *P. pullata* group is interesting. The body colour resembles that of *pullata,* the spination, that of *prativaga* and the annulation is absent, as in *pullata* specimens. Again, for some of the measured morphological characters the *fulvipes* subgroup may be classed in the *pullata* subgroup (length of the cephalothorax in females, width of the cephalothorax in males, length of the first (females) and fourth (males) legs. In other respects *fulvipes* resembles *prativaga* (length of the lowest part of the septum and the formula ac^2/db^2 (females: epigyne), and the ratio of the length of the fourth and that of the first leg). The subgroup *fulvipes* takes a separate position with respect to still other features (width and height of the epigyne, length of the septum, ratio of length and width of cephalothorax, cephalothorax length (males), length of the first (males) and fourth (females) leg). So, the *fulvipes* subgroup is to some extent morphologically intermediate between the other subgroups. This may be due to the special type of habitat of the populations of the *fulvipes* subgroup. Dahl (1908) stated that *fulvipes* only occurs in peat moor swamps. In Norway and Finnland *fulvipes* occurs in the same biotopes as *prativaga* (Palmgren, 1939; Tambs-Lyche, 1939). In these areas, too, morphological differences between *prativaga* and *fulvipes* are small. Both authors report that, within the same populations, specimens occur with annulated, partly annulated and not annulated legs. They suggest that the separation into two ecotypes has not (yet) occurred in the countries studied. Petrusewicz (1935) reports that a continuous variation between the forms *prativaga* and *fulvipes* occurs in the eastern part of Poland, but not in the western part. In the Netherlands the situation is comparable with that in Germany and the western

part of Poland: in all peat moor swamps in the eastern part of the Netherlands (e.g. Steenwijk, Nijmegen and Winterswijk) *fulvipes* is found. Besides, outside the peat moor swamps *fulvipes* has not yet been found. Continuous variation of the annulation of the legs does not occur in *prativaga*.

Obviously, a more detailed description of the habitat of several populations of the *P. pullata* group is necessary. Such a description, together with an ecological investigation of the populations, will possibly contribute to the solution of the above problems.

Summary

477 females and 125 males of the *P. pullata* group were sampled from several populations in the Netherlands. The specimens were separated into the *pullata, prativaga* and *fulvipes* subgroups. This separation, being based exclusively on body colour, was supported by recordings of the spinosity and the annulation of the first leg. Measurements of the cephalothorax, the first and the fourth leg and the epigyne resulted in the following conclusions.

(1) Frequency distributions of each of the characters measured show considerable overlap both within and between the respective subgroups.

(2) Significant differences exist between samples within subgroups and between samples from different subgroups.

(3) Within the *P. pullata* group two groups of samples are distinguished which correspond to the *prativaga* and the *pullata* subgroups. It is suggested that specimens of these two groups of populations use the habitat in a different way but that interbreeding occurs in mixed populations.

(4) The position of the *fulvipes* subgroup in the *P. pullata* group is interesting. A comparison has been made with the situation in Germany, Poland, Norway, and Finnland.

(5) A detailed study of the differences and similarities between the populations of the *p. pullata* group in ecological, ethological, and genetical respect is needed to evaluate the distinct species, subspecies or forms within the *P. pullata* group.

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